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Modelling landscape constraints on farmland bird species range shifts under climate change

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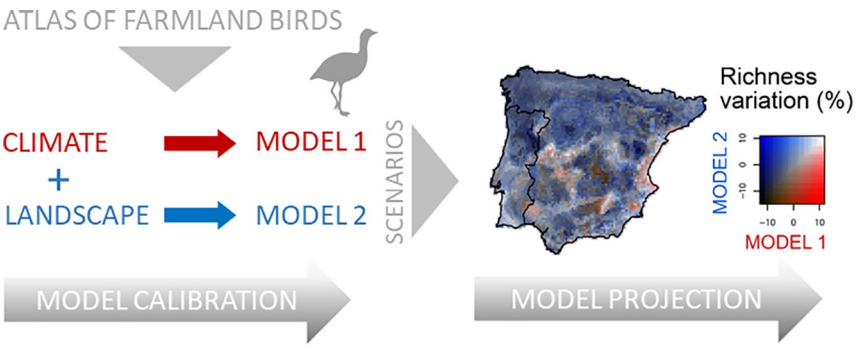
HIGHLIGHTS

- Climate-only and climate plus landscape models yielded different future species range shifts.
- Different models also predicted contrasting geographical patterns of change in species richness.
- Habitat farmland specialists tend to expand, whereas generalist to retract under the same scenarios.
- Predicted expansions under climate change scenarios are severely constrained by predicted landscape changes.
- Incorporating landscape factors is crucial to forecast range shifts of farmland habitat specialists.

GRAPHICAL ABSTRACT



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ABSTRACT

Several studies estimating the effects of global environmental change on biodiversity are focused on climate change. Yet, non-climatic factors such as changes in land cover can also be of paramount importance. This may be particularly important for habitat specialists associated with human-dominated landscapes, where land cover and climate changes may be largely decoupled. Here, we tested this idea by modelling the influence of climate, landscape composition and pattern, on the predicted future (2021–2050) distributions of 21 farmland bird species in the Iberian Peninsula, using boosted regression trees and 10-km resolution presence/absence data. We also evaluated whether habitat specialist species were more affected by landscape factors than generalist species. Overall, this study showed that the contribution of current landscape composition and pattern to the performance of species distribution models (SDMs) was relatively low. However, SDMs built using either climate or climate plus landscape variables yielded very different predictions of future species range shifts and, hence, of the geographical patterns of change in species richness. Our results indicate that open habitat specialist species tend to expand their range, whereas habitat generalist species tend to retract under climate change scenarios. The effect of incorporating landscape factors were particularly marked on open habitat specialists of conservation

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concern, for which the expected expansion under climate change seems to be severely constrained by land cover change. Overall, results suggest that particular attention should be given to landscape change in addition to climate when modelling the impacts of environmental changes for both farmland specialist and generalist bird distributions.

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1. Introduction

Many studies have attempted to estimate the future effects of global environmental changes on biodiversity (e.g., Thuiller et al., 2005; Araújo et al., 2006; Garcia et al., 2011). Many of these studies examine the effect of climate change alone, leaving aside the effects of non-climatic drivers (e.g., Harfoot et al., 2014; Morelli and Tryjanowski, 2015; Titeux et al., 2016). However, the effects of climate change on biodiversity can be influenced by interactions with other components of global change (e.g., Clavero et al., 2011; Hof et al., 2011; Maxwell et al., 2016), particularly with land use changes and related effects on other pressures such as water regime (e.g., Jetz et al., 2007; Rosenzweig et al., 2008; Thuiller et al., 2014a; Newbold et al., 2016).

Both climate and land cover changes are considered major drivers of global biodiversity change (Sala et al., 2000; Jetz et al., 2007; de Chazal and Rounsevell, 2009). However, climate is often regarded as the most important driver at large spatial extents and coarse spatial resolutions (e.g., Thuiller et al., 2004a; Luoto et al., 2007; Triviño et al., 2011). The relative contribution of climate and land cover on future species range shift projections remain poorly explored (Pearce-Higgins and Green, 2014; but see studies from Table S1, Appendix A). Previous studies have found that land cover can be correlated with climate and that including land cover variables did not improve the accuracy of species distribution models, as expected (e.g., Seoane et al., 2003; Thuiller et al., 2004a; Triviño et al., 2011; Reino et al., 2013). Although climate and land cover are generally correlated, however, climate does not necessarily fully control land cover, which may be affected by a number of additional factors such as soil type, topography, socio-economic contexts and policies (Veldkamp and Lambin, 2001; Ribeiro et al., 2014, 2016). In addition, because climate and land cover often play key roles at different spatial scales (Pearson et al., 2004), they are likely to show different geographical patterns of change and hence may affect different regions in a distinct way. Moreover, climate and landscape drivers may interact in their effect on species geographical range, because the two drivers may have different effects on different groups of species (Opdam and Wascher, 2004; Sohl, 2014; Jarzyna et al., 2015).

Most studies modelling the consequences of changes in the structural component of landscape have ignored potentially important processes related to landscape fragmentation (e.g., Vallecillo et al., 2009; Triviño et al., 2011), although they have been shown to be determinant for some species (Jarzyna et al., 2015). This is the case, for instance, of some farmland bird specialists that were shown to be very sensitive to habitat fragmentation at several spatial scales (Reino et al., 2009; Reino et al., 2013). There is a well-established idea that generalist species tend to cope better with environmental changes than specialist species (Gilman et al., 2010; Clavel et al., 2011; Davey et al., 2012; Lurgi et al., 2012; Case et al., 2015). However, at the same time, some studies point to an idiosyncratic nature of species responses to climate change, making it difficult to draw generalizations (e.g., Mair et al., 2012; Moritz and Agudo, 2013; Sohl, 2014). For example, in a recent study, Princé et al. (2015) found that the relative sensitivity of farmland bird specialists and generalists to climate and land cover changes varied among the different global change scenarios that were considered.

Here we model the relative importance of changes at the landscape level on range shifts predictions under future environmental change scenarios, aiming at bringing new insights on the interplay of three component of the environment: biosphere, atmosphere and anthroposphere. We focused on farmland birds in the Iberian Peninsula, considering both climate change and changes in land cover and landscape structure, mainly as the result of land abandonment and changes in agricultural practices, associated with three socioeconomic scenarios for the period of 2021 to 2050. We hypothesize that taking into account changes in landscape composition and structure will potentially strongly affect predictions of farmland bird geographical ranges under climate change scenarios. We also expect that the potential impacts of landscape changes on farmland bird geographical ranges is dependent on the degree of habitat specialization (Clavel et al., 2011), namely the association to farmland landscapes. The overarching goal of this study is thus to examine the proposition that landscape changes should be accounted for when forecasting the effects of environmental changes on the distribution of species highly sensitive to landscape structure.

2. Material and methods

2.1. Data

We used distributional records for 21 Iberian farmland bird species (Table 1), obtained from the most recent breeding bird atlas from Spain (Martí and Moral, 2003) and Portugal (Equipa Atlas, 2008), reporting the occurrence of bird species in 5923 10 × 10 km resolution UTM cells. These are the highest-resolution bird distribution data available for Iberia. Farmland birds selected for this study include species with different degrees of habitat specialization to open habitats, because these seem to be those most at risk from ongoing changes in agricultural land cover. Some of the species are highly specialized to open grassland habitats (e.g., Calandra lark *Melanocorypha calandra*), whereas others can tolerate different degrees of habitat fragmentation (e.g., Little bustard *Tetrax tetrax*), or are often considered habitat generalists (e.g., Corn bunting *Emberiza calandra*). Nonetheless, most of the

Table 1
Discrimination power as measured by the mean cross-validation AUC among the nine combinations of BRT settings, and respective standard deviation, of distribution models developed for each farmland bird species using either climate variables and both climate and landscape variables. In each case we indicate the percent variation of mean AUC for climate + landscape models in relation to climate only models.

Species	Climate	Climate + landscape	% AUC variation
Falco naumanni	0.878 (0.0005)	0.888 (0.0005)	1.16
Circus pygargus	0.820 (0.0017)	0.859 (0.001)	4.68
Tetrax tetrax	0.852 (0.0014)	0.882 (0.0007)	3.42
Otis tarda	0.867 (0.0015)	0.889 (0.0011)	2.53
Coturnix coturnix	0.774 (0.0023)	0.804 (0.0013)	3.89
Pterocles alchata	0.933 (0.0011)	0.941 (0.0007)	0.89
Pterocles orientalis	0.859 (0.0008)	0.884 (0.0009)	2.93
Burhinus oedicnemus	0.852 (0.0011)	0.876 (0.0012)	2.82
Coracias garrulus	0.846 (0.0011)	0.856 (0.001)	1.21
Alauda arvensis	0.868 (0.0003)	0.871 (0.0004)	0.28
Anthus campestris	0.846 (0.0006)	0.851 (0.0008)	0.60
Lullula arborea	0.839 (0.0005)	0.851 (0.0004)	1.49
Melanocorypha calandra	0.885 (0.0006)	0.909 (0.0004)	2.69
Calandrella brachydactyla	0.824 (0.0005)	0.842 (0.0007)	2.11
Calandrella rufescens	0.947 (0.0009)	0.947 (0.0007)	0.06
Galerida cristata	0.908 (0.0006)	0.925 (0.0004)	1.86
Galerida theklae	0.869 (0.0012)	0.877 (0.0012)	0.90
Chersophilus duponti	0.919 (0.0009)	0.928 (0.0007)	0.87
Oenanthe hispanica	0.856 (0.0006)	0.861 (0.0009)	0.55
Carduelis cannabina	0.793 (0.0015)	0.801 (0.0017)	0.97
Emberiza calandra	0.892 (0.0007)	0.913 (0.0006)	2.29

farmland species considered may tolerate a wide range of habitats, though we excluded species which are often associated with tree-cover habitats (e.g., red-legged partridge *Alectoris rufa*). For each species, the mean landscape Shannon diversity index in the occurrence cells, based on the forty-four land cover classes from CORINE (EEA, 2000), was computed and the resulting values, after rescaling between 0 and 1, were inverted. We used the resulting index, here referred to as Landscape Specialization Index (LSI), as a surrogate of habitat specialization (see Table 1). A significant negative relationship between bird's habitat specialization and landscape fragmentation derived from CORINE land cover maps was shown elsewhere (Devictor et al., 2008).

We used three climatic variables that synthetize two factors – energy and water – that determine biological diversity distribution worldwide (Hawkins et al., 2003): average minimum temperature of the coldest month, average mean maximum temperature of the hottest month and average total annual precipitation. A fourth selected climatic variable - standard deviation of monthly means of minimum temperature – reflected seasonality of climate. The baseline climatic data was obtained from the Portuguese and Spanish meteorological agencies (IM and AEMET, respectively), interpolated to a UTM 10 × 10 km grid (Araújo et al., 2012).

The future climate was based on the scenarios developed in the ALARM project (http://www.alarmproject.net/alarm, Assessing Large-scale Environmental Risks for biodiversity with tested Methods; Settele et al., 2005), resampled at a 10-min resolution (~16 km at the latitude of the study). Future scenarios of climate and land cover for the period 2021–2050 were based on the three alternative storylines developed in the ALARM project: 1) "Business As Might Be Usual" (BAMBU based on the A2 scenario from the IPCC), 2) "Growth Applied Strategy" (GRAS based on the A1F1 scenario from IPCC) and 3) "Sustainable European Development Goal" (SEDG based on the B1 scenario from IPCC). These scenarios covered a broad range of potential socio-economic, political, technological and geobiosphere changes, and were developed to describe alternative future pathways of key driving factors affecting biodiversity (Araújo et al., 2008; Dendoncker et al., 2006; Rounsevell et al., 2006; Spangenberg, 2007; Spangenberg et al., 2012). The future land cover change scenarios were based on the Coordination of Information on the Environment (CORINE Land Cover; European Environmental Agency, 2002, see Rounsevell et al. (2006) and Dendoncker et al. (2007) for methodology details). The forty-four land cover classes from CORINE were aggregated into six classes for these scenarios: *Urban*, *Cropland*, *Permanent crops*, *Grassland*, *Forest*, and *Others*. We assumed that *Cropland* was the class encompassing the most suitable habitats for the selected Iberian farmland bird species. For both future scenarios and the baseline period, the *Cropland* class resulted from aggregation of the following CORINE classes: 1) Non-irrigated arable land; 2) Permanently irrigated land; 3) Rice fields; and 4) Complex cultivation patterns. The *Grassland* class was not considered as a relevant land cover aggregation for farmland bird species because it is overly abundant in Portugal due to a somehow arbitrary amalgamation of several land cover types (for example, the category "Land principally occupied by agriculture with significant areas of natural vegetation" was included in the *Grassland* category).

Future climatic scenarios were downscaled to the same 10-km grid cell resolution of the baseline data. For both baseline period and future land cover scenarios, we assumed that the quantity of suitable habitat for farmland birds is strongly influenced by the percentage of the grid cells covered with the class *Cropland*. We computed three landscape fragmentation metrics on the distribution of croplands for each 10 × 10 km UTM grid cell of Iberian Peninsula, following the approach used in a previous study (Reino et al., 2013). Landscape metrics comprised three variables: mean cropland patch area, number of cropland patches, and edge density. We computed edge density, i.e. edges between patches of different classes, using the total edge length of cropland patches at each grid square. The computation of the percentage of cropland area and the three landscape metrics at each 10 km grid cell were based on land cover raster themes with 100 m resolution. We carried out the analyses in ArcGIS 9.3 (ESRI, 2011).

Because birds' data were restricted to the Iberian Peninsula, arguably the models may fail to capture the full range of suitable conditions of each species. This may cause truncated response curves at extreme conditions and, consequently, biased projections (Thuiller et al., 2004b). To evaluate this potential effect, we mapped the grid cells that in the future would lay outside the training conditions for each climatic variable. Only for the BAMBU scenario and one variable (Mean Maximum Temperature), a considerable extension of the Iberian Peninsula (24,7% of the grid cells) was predicted to be outside the baseline range of values. For the remaining variables, extrapolation area represented <5% of the grid cells. For the GRAS and SEDGE scenarios, the extrapolation area represented, respectively, <2% and 1% for all climatic variables. All extrapolation areas showed warmer and drier climates. Because all species occur in North Africa we can assume that climate projections will not go beyond species tolerances. Nevertheless, this potential problem was duly considered when interpreting our modelling results, though violation of such assumption would mainly affect the high-end scenario (BAMBU). Regarding landscape structure, given the high structural heterogeneity of Iberian landscape we can assume that a sufficient broad gradient is covered in the baseline.

2.2. Statistical modelling

We developed boosted regression trees (BRT) (Friedman et al., 2000; Hastie et al., 2001) to estimate the relationship between the 21 Iberian farmland birds and the climatic and landscape variables for the baseline period. We then used the resulting relationships to project the potential distributions under the three future climate and land cover change scenarios for 2021–2050. BRT differs from the traditional classification and regression tree techniques that produce a single 'best' tree, by making use of a 'boosting' technique to combine large numbers of relatively simple tree models adaptively, in order to optimize predictive performance (see e.g., Elith et al., 2008; Leathwick et al., 2006, 2008 for further details). The main difference between BRT and other tree-based ensemble techniques (e.g., random forests; Prasad et al., 2006) is that trees are fitted sequentially through a stagewise process, i.e., at each step of model development, the trees from previous steps are left unchanged as the model is enlarged (Elith et al., 2008). This relative model rigidity, where the overall hierarchical structure of variable effects is maintained stable, is an important feature for the purpose of our study, which focuses on two very different sets of variables (climate and landscape) that are expected to act hierarchically on species distributions (Pearson et al., 2004). Furthermore, BRT are recognized for their capabilities to reliably selected meaningful variables, through automatic detection of interactions and robust fitting of trends (Hastie et al., 2001). BRT has also the advantage of handling different types of variables, and coping with collinearity and non-linear relationships between predictors (Elith et al., 2008).

To optimize the number of trees in each BRT model, we carried out a stepwise process based on 10-fold cross-validations using mean deviance on the validation data as a measure of predictive performance (Elith et al., 2008). Two important parameters must be defined a priori to determine the number of trees required for optimal predictions: the learning rate, which determines the contribution of each tree to the growing model, and the tree complexity that controls the number of interactions among variables (i.e., the number of splits of individual trees). We used three alternative values for both tree complexity and learning rate to account for the uncertainties introduced by the subjectivity of the previously selected parameter values. To select a range of learning rate and tree complexity values ensuring that at least 1000 trees were achieved after the stepwise process (Elith et al., 2008), we first trained the data using several alternative learning rate and tree complexity values. We finally set learning rate values to 0.002, 0.003

and 0.004 and tree complexity values to 3, 4 and 5. Discrimination power of models was assessed by computing the mean Area Under the Receiver Operational Curve (AUC; Fielding & Bell, 1997) based on 10-fold cross-validations. BRT were computed with the gbm (Ridgeway, 2013) and dismo (Hijmans et al., 2012) libraries in R software version 2.15.2 (R Development Core Team, 2013).

To assess the impact of including landscape variables in the predictions of distribution expansion/retraction of species, we fitted two different models per species for each learning rates and tree complexity combination: a climate-only model and a climate + landscape model. For each kind of model, the probabilities of occurrence from the nine models resulting from the pairwise combination of learning rates and tree complexity values were averaged following standard committee averaging procedures in ensemble modelling (Araújo and New, 2007). The importance of each variable to the model was based on the measure of relative influence described in Friedman (2001) and averaged across the nine models.

2.3. Range shifts

We classified the probabilities of occurrence obtained with the BRT models into potential presence/absence maps for the baseline period and for the period of 2021–2050 under the three alternative scenarios hypothesis. The probability value that maximized the sum of sensitivity and specificity was used as the cut-off point for discriminating predicted presence and absence (Liu et al., 2005).

Using the resulting maps of the potential species distributions we computed the net variation of the geographical range for both climate-only and climate + landscape models (% of variation of the predicted species prevalence relative to the baseline), between the baseline and the future scenarios. We also computed the difference of the range variation between climate-only and climate + landscape models to assess if the inclusion of landscape variables led to a weaker/stronger range retraction or weaker/stronger range expansion. We tested the correlation between the Landscape Specialization Index for each species and both the variation of the geographical range area and the difference of the range area variation between climate-only and climate + landscape models. We computed the number of winner species (i.e. species that are currently absent but predicted to be present in the future) and of loser species (i.e. species that are currently present but predicted to be absent in the future) in each grid cell based on the differences between species presence/absence maps for the baseline and each future scenario predictions. To test differences among the three scenarios in the resulting maps, we used a modified version of the *t*-test to assess correlation between two spatial processes (Clifford et al., 1989) implemented in the SpatialPack R package (Osorio et al., 2012).

3. Results

3.1. Model performance

The incorporation of landscape variables in the climate-based models consistently improved model's discrimination ability, as measured with mean cross-validation AUC values (Wilcoxon signed rank test, $p < 0.001$). However, the contribution of landscape variables did not increase substantially the discrimination ability of models, with percent (%) of improvements varying from 0.06% for *Calandrella rufescens* to 4.68% for *Circus pygargus* (Table 1). The species Landscape Specialization Index was positively correlated with AUC values of both the climate-only (Pearson $r = 0.49$, $p < 0.05$) and climate + landscape models (Pearson $r = 0.51$, $p < 0.02$). However, habitat specialization was not correlated with the percentage increase of discrimination ability (Pearson $r = -0.08$, $p = 0.74$).

3.2. Variable importance

The climatic variables with the highest relative influence in the models were the average minimum temperature of the coldest month and the average mean maximum temperature of the warmest month (Table 2). The importance of these two variables showed no significant correlations with the species Landscape Specialization Index (mean maximum temperature, Pearson $r = 0.06$, p-value $= 0.80$; mean maximum temperature, Pearson $r = -0.16$, p-value $= 0.48$). Among the landscape variables, the mean cropland patch area followed by the edge density were found to be the most influential for all the species, independently of their degree of specialization.

3.3. Range shifts

The direction of projected range shifts for 17 out of 21 farmland bird species were consistent among the three socio-economic scenarios. Among these, range expansion was predicted for 10 species and range contraction was predicted for 7 species (Table 3).

Overall, the strongest influence of landscape variables in range shifts, were found for species predicted either to show stronger retraction or weaker expansion of their geographical range (Table 3). The maximum variation in the percentage of range shift change was found for *Otis tarda* (e.g., −158.8% for the GRAS scenario) and *Pterocles alchata* (e.g., 151.0% for the GRAS scenario). For the three scenarios, no significant correlations were found between the percentage of increase in the discrimination ability of models and the percentage of predicted range shift changes after considering landscape variables (Pearson's correlation, $r < 1$ and $p > 0.6$ for all scenarios).

When the outputs of climate + landscape models were related with the species' degree of habitat specialization, as given by the Landscape Specialization Index (LSI), some general trends on the predicted range shifts emerged. The relationship between predicted range shifts and LSI indicates a tendency from range retractions to range expansions for increasing species' habitat specialization (Fig. 1). This positive correlation was significant (Pearson's correlation, $p < 0.05$) for all scenarios in the case of climate-only models. In the case of climate + landscape models, the correlation was significant for the GRAS scenario, whereas for the BAMBU and SEDGE scenarios the relationships were only marginally significant (Fig. 1).

A significant negative relationship between LSI and the variation of range shift percent change after including landscape variables in the models (i.e. the difference between the percent change of range shift in the climate-only model and the percent change of range shift in the climate + landscape model), was found for the three scenarios (Pearson's correlation, $p < 0.05$; Fig. 2). For increasing LSI values, a tendency for the percentages of change to be more negative was found, i.e., as the degree of species habitat specialization increases, climate-only models tended to be more over-optimistic in comparison to climate + landscape models.

3.4. Species richness

The mean number of farmland bird species per 10 × 10 km UTM grid cell was forecasted to be significantly higher in the future under any of the three socioeconomic scenarios than at present (Wilcoxon signed rank test, $p < 0.001$). However, the average absolute increase in local species richness was significantly lower using the climate + landscape model than the climate-only model under the BAMBU (0.48 species ± 3.16 SD vs. 1.43 species ± 3.74 SD), GRAS (0.20 species ± 3.34 SD vs. 1.31 species ± 3.83 SD) and SEDGE (0.59 species ± 3.21 SD vs. 1.68 species ± 3.65 SD) scenarios. There were also differences between models in the spatial pattern of absolute variation in local species richness. Generally, climate-only models tended to predict larger areas of richness increase in both central and southern Iberia, while climate + landscape models tended to predict larger areas of richness increase in Northern Iberia (Fig. 3). Consistent increases in species richness were

Table 2
Mean importance of variables in the climate + landscape BRT model (grey intensity reflects variable importance). Crop – presence/absence of cropland; Edge - edge density; MPA - mean cropland patch area; NUMP - number of cropland patches; Prec - average total annual precipitation; Tmax - average mean maximum temperature; Tmin - average minimum temperature of the coldest month; Tmin SD - minimum temperature standard deviation.

Species	Crop	Edge	MPA	NUMP	Prec	Tmax	Tmin	Tmin SD
F. naumanni	0.01	6.07	25.99	2.11	9.42	36.63	6.95	12.83
C. pygargus	0.02	8.96	9.51	3.20	12.55	21.66	30.92	13.19
T. tetrax	0.00	7.29	7.64	2.25	13.03	17.18	38.40	14.22
O. tarda	0.00	7.28	14.45	2.29	10.25	43.23	8.57	13.92
C. coturnix	0.11	9.05	13.04	2.85	15.51	18.99	23.19	17.26
P. alchata	0.00	7.33	22.84	2.85	12.89	28.47	7.72	17.89
P. orientalis	0.00	8.23	21.08	2.76	10.16	36.25	8.39	13.13
B. oedicnemus	0.01	6.68	7.22	2.71	9.87	22.31	40.24	10.97
C. garrulus	0.00	6.58	9.76	2.06	12.82	20.12	30.43	18.24
A. arvensis	0.05	3.47	3.85	1.87	11.79	18.48	48.09	12.39
A. campestris	0.01	5.20	6.31	2.16	13.65	23.29	34.99	14.38
L. arborea	0.04	4.13	11.91	2.96	13.68	24.34	24.89	18.05
M. calandra	0.00	4.47	8.25	1.55	9.18	31.46	34.58	10.51
C. brachydactyla	0.01	6.61	7.58	2.34	8.28	17.38	47.51	10.30
C. rufescens	0.00	7.17	8.22	5.24	9.84	15.52	43.01	11.00
G. cristata	0.02	4.55	6.53	1.06	7.08	8.41	64.70	7.65
G. theklae	0.01	4.34	5.69	1.51	10.05	19.26	46.36	12.78
C. duponti	0.00	9.64	12.21	7.45	13.41	18.58	23.26	15.45
O. hispanica	0.01	3.73	5.64	3.23	8.68	18.94	46.28	13.49
C. cannabina	0.05	7.99	21.67	3.11	12.69	25.17	12.00	17.32
E. calandra	0.09	5.06	13.40	1.87	10.57	49.40	8.73	10.89

Table 3
Differences between the range shifts predicted by species distribution models based on climate alone and on climate + landscape for the three future ALARM storyline scenarios. Values indicate the additional percentage of change introduced when landscape variables are also considered in the models. Symbols denote the direction of the range change of the climate/landscape and whether the model based on climate/landscape predicts stronger or lower changes than model based on climate alone. ▽ - weaker retraction; ▼- stronger retraction; △ - weaker expansion; ▲ - stronger expansion.

Species	Additional % change					
	BAMBU		GRAS		SEDGE	
Falco naumanni	−21.2	△	−8.0	△	−33.0	△
Circus pygargus	−14.4	△	−17.7	△	−12.7	△
Tetrax tetrax	−20.6	△	−25.0	△	−21.0	△
Otis tarda	−132.6	△	−158.8	△	−138.7	△
Coturnix coturnix	−40.8	▼	−44.8	▼	−42.7	▼
Pterocles alchata	−121.5	▼	−151.0	△	−132.6	▼
Pterocles orientalis	−58.1	▼	−73.3	▼	−74.5	▼
Burhinus oedicnemus	−28.2	△	−29.7	△	−28.4	△
Coracias garrulus	14.6	▲	23.6	▲	7.5	▲
Alauda arvensis	1.9	▽	3.9	▽	−0.9	▼
Anthus campestris	−21.2	▼	−33.7	▼	−22.6	▼
Lullula arborea	37.1	▲	44.9	▲	40.6	▲
Melanocorypha calandra	−9.1	△	−3.9	△	−16.5	△
Calandrella brachydactyla	10.7	▲	13.4	▲	8.0	▲
Calandrella rufescens	−45.4	△	−29.5	△	−58.0	△
Galerida cristata	7.3	▽	1.3	▽	12.9	▽
Galerida theklae	20.3	▽	21.2	▽	22.5	▽
Chersophilus duponti	−0.8	▼	2.7	▽	1.2	▽
Oenanthe hispanica	10.1	▽	9.7	▽	19.4	▽
Carduelis cannabina	2.4	▲	4.2	▽	−1.0	△
Emberiza calandra	−2.2	▼	−3.3	▼	−4.8	▼

predicted to occur irrespective of model type in central and southern Iberia.

3.5. Losers and winners

The geographical patterns of loser and winner species per 10 km grid square were also largely dependent on whether landscape variables were included or not in the models (Fig. 4). Significant correlations among the three climate change scenarios were found for both winners and losers maps, even after accounting for spatial autocorrelation (modified *t*-test, $p < 0.001$). Climate-only models predicted a larger area with high numbers of winner species (Fig. 4, left maps, yellow areas), mainly in the centre, southern Iberian mountain ranges and the eastern coast. Contrarily, climate + landscape models predicted a larger area showing high numbers of loser species, mainly in the southern plains (Fig. 4, right maps, blue areas).

4. Discussion

Our results confirm the hypothesis that the inclusion of landscape variables in species distribution models strongly affect range shift predictions of Iberian farmland birds, despite a generally low contribution to models' performance. Overall, the resulting species distribution models predict that habitat specialists will tend to expand their range, whereas generalists will tend to retract under climate change scenarios. However, in many cases, the inclusion of landscape variables in the models leads to an attenuation of the projected range expansion of specialist species under scenarios of both climate and landscape changes.

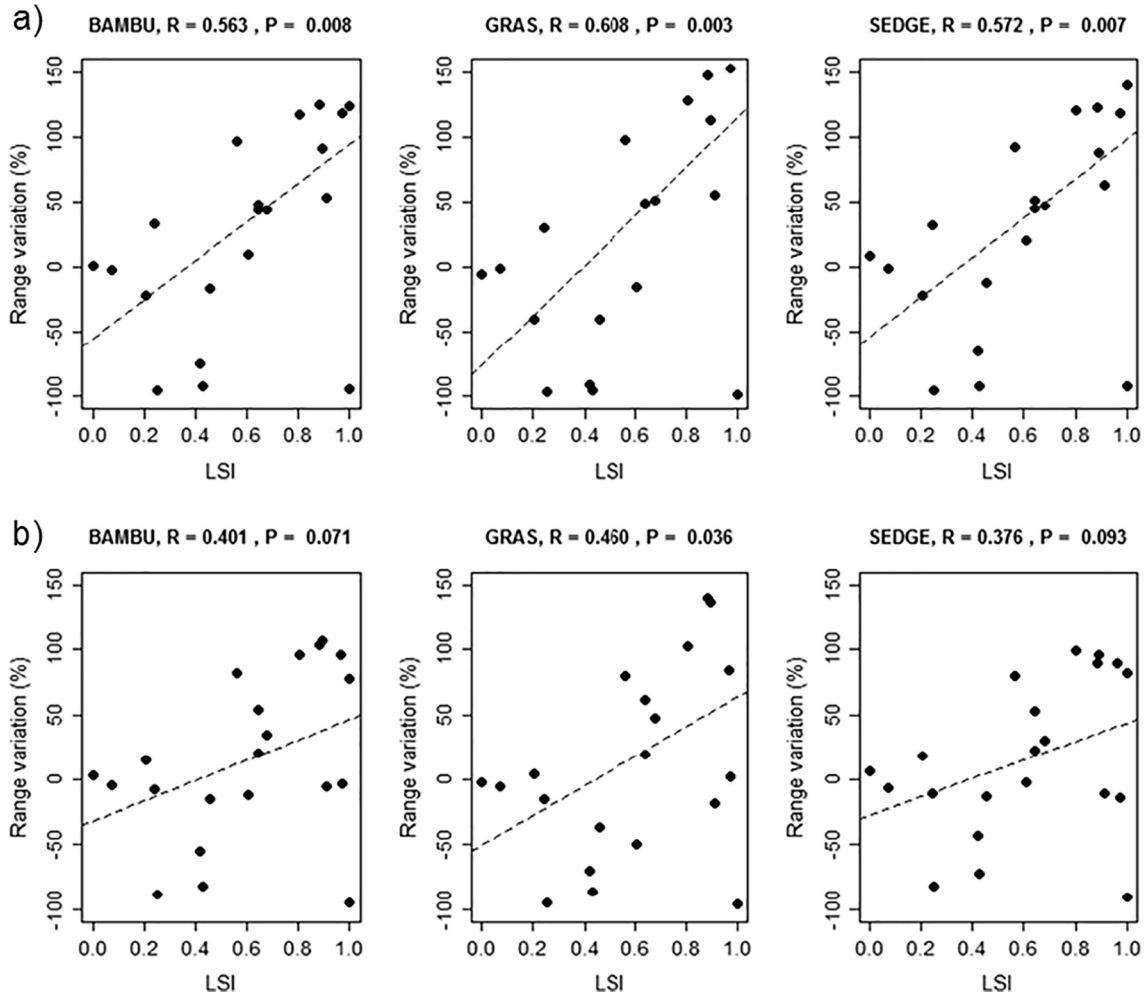
a)
BAMBU, R = 0.563 , P = 0.008
GRAS, R = 0.608 , P = 0.003
SEDGE, R = 0.572 , P = 0.007
b)
BAMBU, R = 0.401 , P = 0.071
GRAS, R = 0.460 , P = 0.036
SEDGE, R = 0.376 , P = 0.093
Range variation (%)
LSI

Fig. 1. Relationship between the species Landscape Specialization Index (LSI) in the presence cells, and the predicted species percent range variation (future) in relation to the baseline modelled range, for the climate-only (a) and the climate + landscape models (b). The Pearson correlation coefficient and the respective *p*-level are shown.

4.1. Impacts of landscape variables on predicted range shifts

Our results are in agreement with other studies that also show a relatively small contribution of landscape related covariates in relation to climate when modelling distributions at coarse spatial resolutions (e.g., Thuiller et al., 2004a; Luoto et al., 2007; Triviño et al., 2011). These findings have supported the view that, for many species, variables such as land cover could sometimes be disregarded from predictive distribution models at wide spatial scales and coarse resolutions (Pearson et al., 2004; Thuiller et al., 2004a; Triviño et al., 2011). Furthermore, the often-found correlation between climate and land cover variables has supported this view (e.g., Thuiller et al., 2004a).

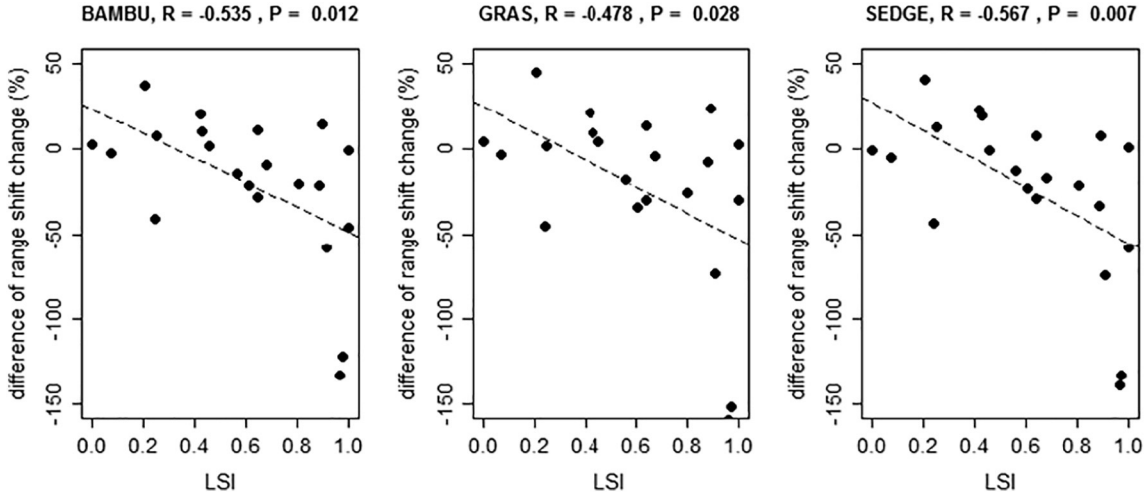

Fig. 2. Relationship between the species Landscape Specialization Index (LSI) in the presence cells and the difference in the percent range shift change predicted by the climate + landscape models in relation to the climate-only models. The Pearson correlation coefficient and the respective *p*-level are shown.

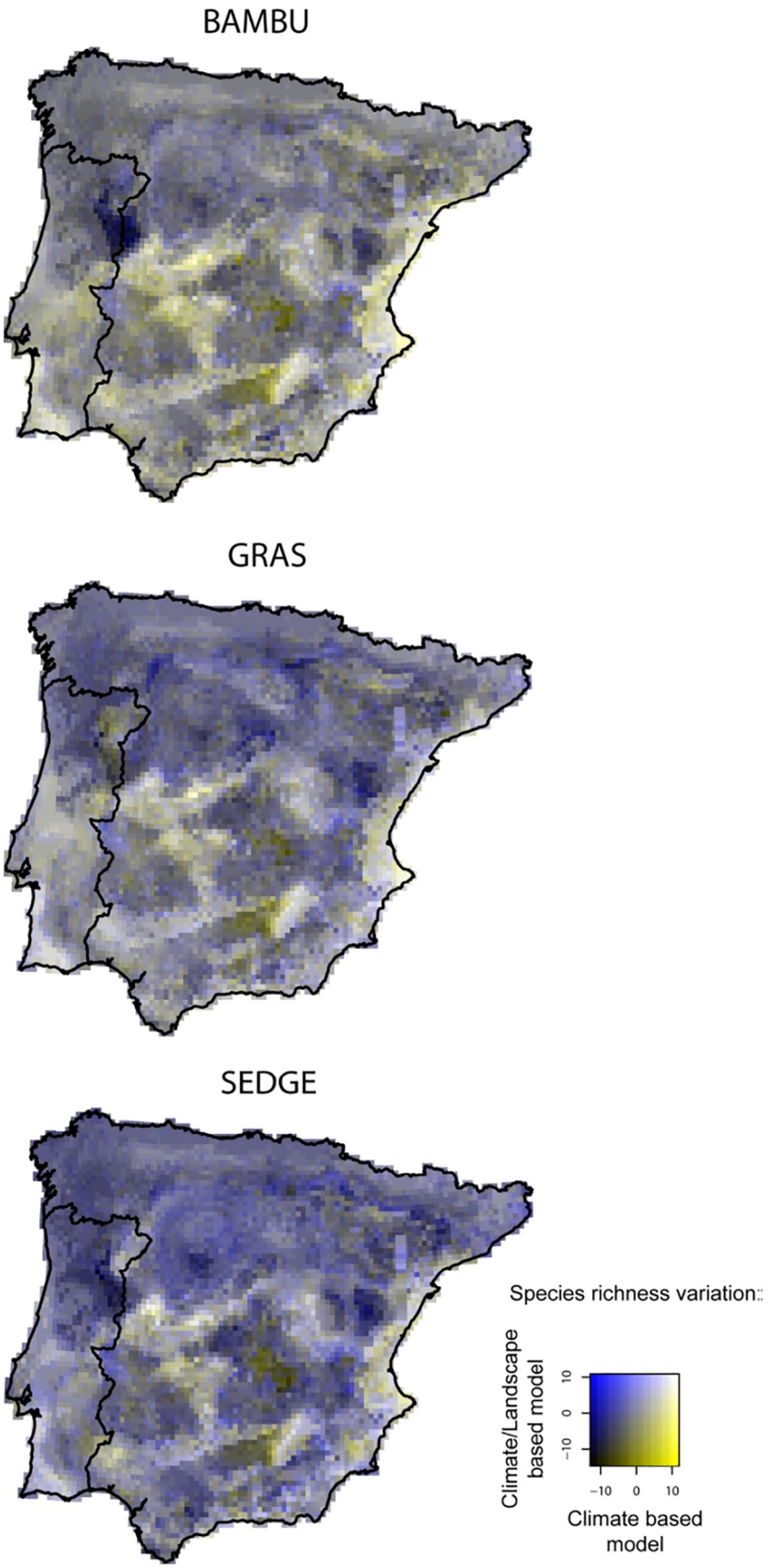

Fig. 3. Bivariate map of species richness percent variation per 10-km grid squares for the three future climate change scenarios. Deviations from the grayscale gradient represent larger richness variations predicted either by climate only-based models (yellow) or by climate/landscape-based models (blue). Brighter tones represent regions with a more positive richness percent variation and darker tones represent regions with a more negative richness percent variation.

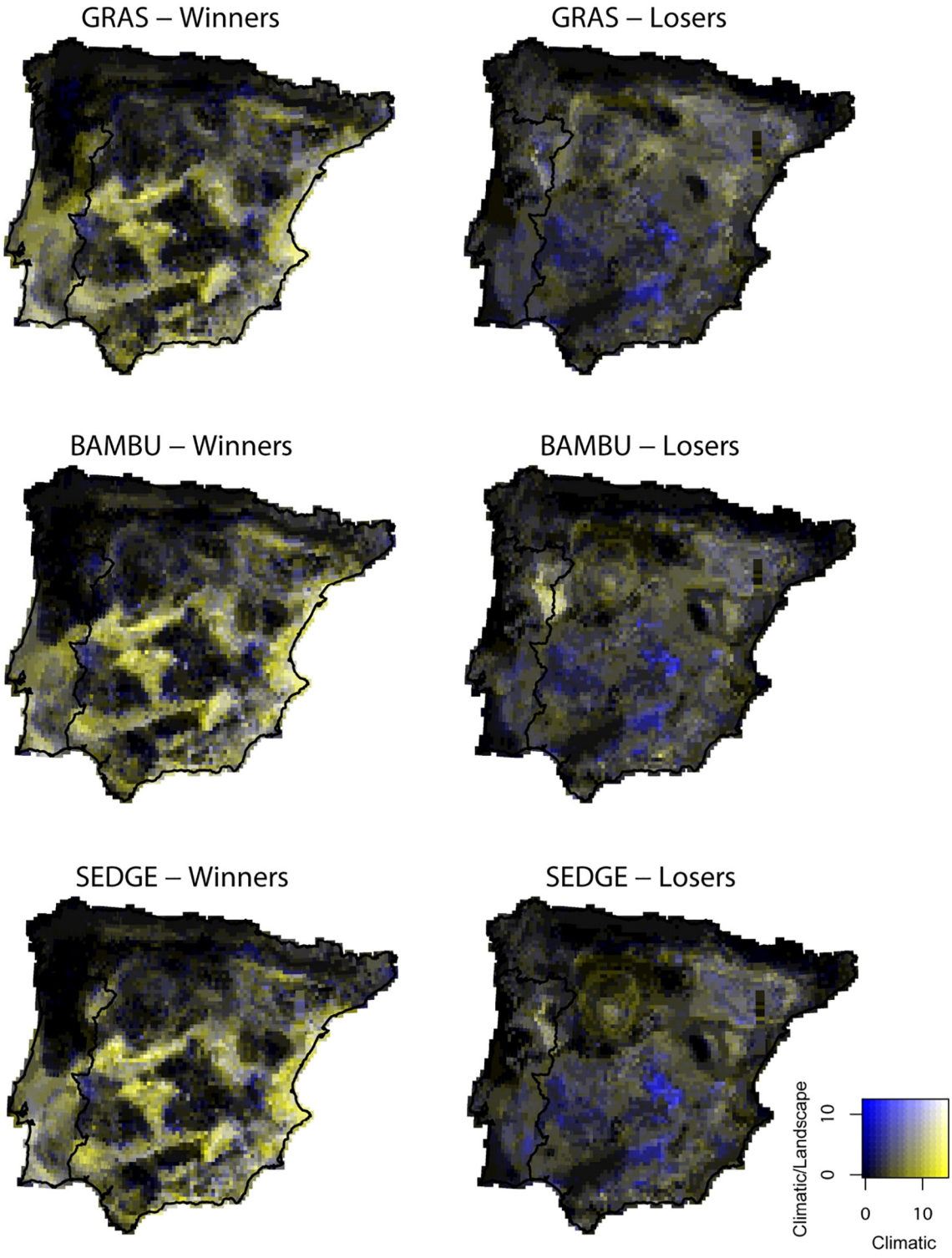

Fig. 4. Bivariate map of the number of loser (left maps) and winner (right maps) species per 10-km grid squares for the three future climate change scenarios. Deviations from the grayscale gradient represent larger number of losers or winners predicted either by climate only-based models (yellow) or by climate/landscape-based models (blue). Brighter tones represent regions with a larger number of winners or losers.

Despite the small explanatory power of landscape metrics, we found that they were associated to major changes on species range shifts under global environmental change. In fact, the addition of landscape variables in the models resulted in deviations up to 150% of the range shift predictions of models using climate alone (Table 3). Landscape changes may occur at a higher pace and magnitude compared to climatic changes and consequently even small contributions to models might result in a noticeable impact on predictions. The significant impact of land use on predictions is also partially in accordance with recent studies that predict large-scale changes in biodiversity (Thuiller et al., 2014a; Princé et al., 2015, Estrada et al., 2016).

Finally, despite their low contribution to models' accuracy, the inclusion of landscape variables also extensively affected predictions of the geographical patterns of richness and of species gains and losses in relation to the climate-only based models. Joint models (climate/landscape) predicted globally more “loser species” and less “winner species” per

grid-square than the climate-only models, resulting in an overall lower predicted mean richness per grid-square. In fact, it has been shown that population changes in farmland birds are often closely related to changes in the intensity of agricultural management rather than to be driven by climatic changes alone (e.g., Pearce-Higgins and Green, 2014). These may implicitly suggest that for the majority of farmland species, recent climate change could still be considered of secondary importance, when compared to changes in agricultural management, which is generally leading worldwide to the intensification of agriculture (e.g., Eglington and Pearce-Higgins, 2012). Even if climatic variables are more determinant according to models of farmland bird distribution, their change in the recent past has been much more subtle than land use changes, which might explain the aforementioned trend.

4.2. The importance of landscape variables along the habitat specialization gradient

The trend found in the projected range shifts along the species' habitat specialization gradient contrasts with the generally accepted idea that generalist species cope better with environmental changes than specialist species (e.g., Clavel et al., 2011). The latter species also appear to have a narrower thermal tolerance, for instance, when compared with more generalist species. This means that habitat change unrelated to climate change may affect species community composition (e.g., Clavero et al., 2011). Nevertheless, the general results of this study are in line with a recent study that found a tendency of generalist bird species occurring in farmlands to be often more affected by climate and land cover changes than specialist farmland birds (Princé et al., 2015). However, strict generalizations can hardly be drawn from our results, which supports the idiosyncratic nature of species responses to climate change (Moritz and Agudo, 2013). In the case of Iberian farmland birds, specialist species are most often adapted to higher temperatures, which might explain the frequent geographic range expansions predicted for these species. However, because habitat specialists are often more dependent of specific habitat conditions this may halt their expansion to other areas with suitable habitat conditions due to habitat and land cover change, for instance.

A major effect of incorporating landscape variables in the models was a less optimistic future for specialist species, mainly with a lower range expansion or, in some cases, a stronger range contraction than predicted by climate-only models. A possible explanation is that, since specialist species tend to be more constrained by both landscape changes and the level of intensity of agricultural management (see Eglington and Pearce-Higgins, 2012), a decrease in landscape favourability in the new expansion areas will counteract with the climatic favourability, resulting in an antagonistic effect between climate and landscape. This is a relevant result for conservation purposes because very often specialist species have an important conservation status and therefore it is crucial to produce more realistic predictions when accounting for the potential effects of climate change (Eglington and Pearce-Higgins, 2012).

Lower expansions after including landscape variables in the models were projected for six non-passerine species (out of nine) and two passerine species. This outcome suggests that for a considerable number of species, including some of the most relevant farmland species of European conservation concern (e.g., little and great bustards and lesser kestrel), future projections based on climatic variables alone might lead to overestimating the expected expansion. Stronger contractions after accounting for landscape changes were predicted only for four species, including three non-passerine species, of which two are of European conservation concern (Black-bellied Sandgrouse and Pin-tailed Sandgrouse), and a passerine species (Corn Bunting). On the contrary, for some species, including some with a relevant conservation status, the incorporation of landscape variables reduced the possibility of a strong range contraction or lead to an increase of the predicted geographical ranges. The set of species in this group included both lark species (crested and Thekla's larks) and two species of European conservation concern (Black-eared wheatear and Dupont's lark). For two Iberian widespread species (skylark and Linnet), at least partially, lower impacts on species range are also expected when landscape variables are included in the models. After accounting for landscape changes, a future range increase was predicted for a few generalist and ecotone-related species. This seems to be the case of the woodlark, which is an open-habitat species associated with more fragmented farmland landscapes, but also of other farmland species like short-toed lark, which is frequent in more fragmented and convoluted landscapes (Reino et al., 2009).

5. Conclusions

This study underpins the need to consider landscape composition and structure when modelling species range shifts under future climate scenarios. This is particularly the case for habitat specialists, which are strongly constrained by habitat availability and configuration. In addition, our models show that specialist species (many with relevant European conservation concern, Table S2) produce less optimistic predictions when landscape changes are also accounted for. The interplay between climate and landscape variables has important implications for an adequate mitigation strategy under climate change. Because farmlands are one of the most extensively modified landscapes and very dependent on management practices and regional policies, the rate, magnitude and direction of alteration is probably more decoupled from climate change than other less altered landscapes. For example, Princé et al. (2015) recently reported that including farmland cover variables could potentially compensate the negative effect of climate change on some species. This means that one needs to be aware when attributing some of the forecasted changes specifically to climate warming (Eglington and Pearce-Higgins, 2012). On the other hand, it also means there is more margin to put into practice management actions that may counteract the negative effects of climate change on bird communities. Our results confirm this idea by showing that more optimistic predictions under climate change for the future are possible when land cover changes are also taken into account. This might suggest that, by implementing right mitigation measures at the landscape level, it would be possible to produce more optimistic predictions for the future, i.e., enlarged range expansions and reduced range contractions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.01.007.

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